Original Article

Unveiling the dynamics of the spider crab *Libinia ferreirae*, through reproductive and population characteristics on the south-eastern coast of Brazil

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Abstract

We investigated the population dynamics of the spider crab *Libinia ferreirae*, focusing on the frequency distribution of individuals in size classes, sex ratio and the action of environmental variables (temperature, salinity, texture and organic matter content in the sediment) on reproduction and recruitment. Monthly collections were made in the Ubatuba region from January 1998 to December 2000. A total of 222 individuals were collected, including 123 juveniles (males and females), 43 adult males, 25 non-ovigerous adult females and 31 ovigerous females. Unlike most adult brachyurans, there was no significant size difference between sexes, and sexual dimorphism seems to be a varying characteristic for this crab genus. The reproductive period and recruitment were continuous with peaks that could be related to water mass dynamics and higher food availability in the Ubatuba region. In addition, our results increase knowledge about part of the life cycle of *L. ferreirae*, which could be useful for comparative studies.

Introduction

Regarding global biodiversity, Brazil is considered an important hotspot area due to the wide variety of environments it contains, whose characteristics can determine the establishment or exclusion of certain organisms (Mantelatto *et al.*, 2016). On the south-eastern Brazilian coast, specifically in the Ubatuba region, there are numerous bays that facilitate the establishment of decapod species by providing shelter/protection and food resources (Furlan *et al.*, 2013).

The high occurrence of these individuals in the Ubatuba region has led to its exploitation, mainly by shrimp fishing (Castilho *et al.*, 2015; Costa *et al.*, 2016; Fransozo *et al.*, 2016). The ecological impacts caused by this activity can destroy benthic communities (Fransozo *et al.*, 2016) through unwanted, frequent and massive capture of accompanying fauna; reduction of habitat complexity (by sediment homogenization); changes in species abundance and distribution, and even the reduction of the asymptotic size of individuals (Kaiser *et al.*, 2002).

In an attempt to minimize these impacts and ensure the conservation and sustainable use of marine resources, the Ubatuba region has been included in a Marine Protection Area (MPA – Cunhambebe Sector) since 8 October 2008, created by the Ministry of the Environment (decree number 53.525). Fishing in this region is only allowed for subsistence of traditional communities, amateurs, and as a leisure activity, while commercial fishing is illegal. In this sense, studies focused on comparing this environment before and after the MPA was implemented are important to determine whether such protection measures are sufficient for conservation.

In the Ubatuba region, spider crabs of the genus *Libinia* Leach, 1815, mainly *Libinia ferreirae* Brito Capello, 1871 and *Libinia spinosa* Guérin, 1832, are frequently caught as by-catch (Bertini *et al.*, 2004, 2010a; Braga *et al.*, 2005; Fransozo *et al.*, 2016; Mantelatto *et al.*, 2016). The species *L. ferreirae* may have a symbiotic relationship with the jellyfish *Lychnorhiza lucerna* Haeckel, 1880 during their larval and juvenile phases (Nogueira Jr & Haddad, 2005; Gonçalves *et al.*, 2016a, 2016b). The association of crabs with jellyfish occurs when the latter go near the ocean floor or when they are dragged by marine currents in contact with the benthic environment (Corrington, 1927; Colombo *et al.*, 2003; Towanda & Thuesen, 2006). Additionally, the megalopa stage could move down and up (Queiroga, 1998) and thus reach the jellyfish. Larval and juvenile individuals may be associated with *L. lucerna* because the latter provide a protected environment during the most vulnerable period of their lives (Nogueira Jr & Haddad, 2005; Gonçalves *et al.*, 2017). Interactions between *L. ferreirae* and individuals of different trophic levels highlight the important ecological functions that this crab has in the marine environment. Therefore, it is essential to understand its population dynamics, since
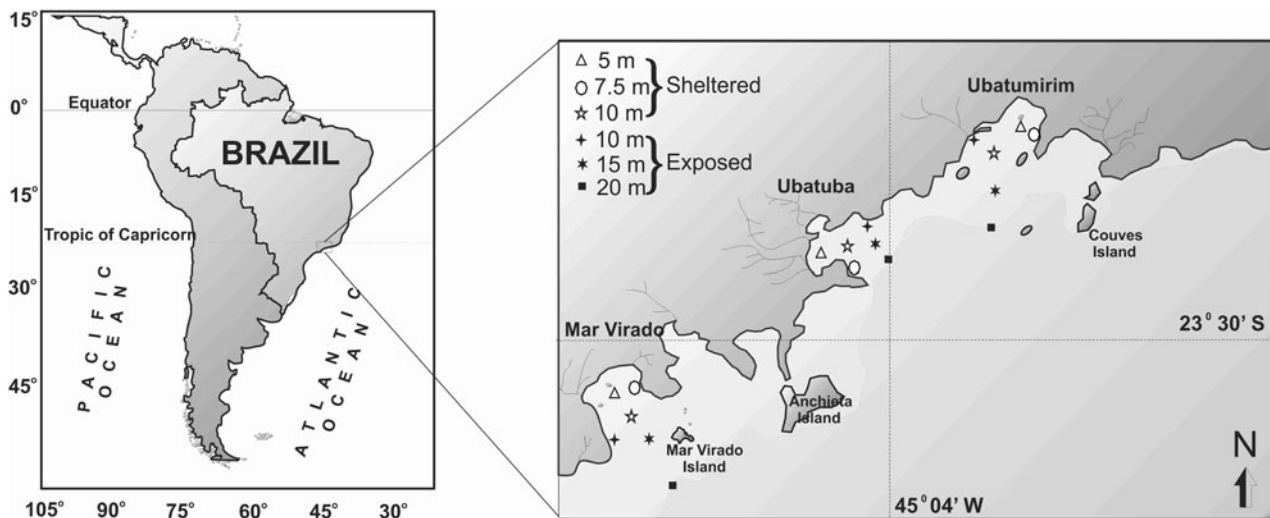
Fig. 1. Map of the Ubatuba region, in the north-eastern coast of São Paulo state, Brazil, showing the three bays (Ubatumirim, Ubatuba and Mar Virado), and their respective sampling stations. Figure adapted from Andrade *et al.* (2014).

these data can generate new information and, consequently, improve mitigating measures that preserve this species.

The population dynamics of crustaceans can be addressed through several aspects, e.g. frequency distribution of individuals in size classes, reproductive period, recruitment, differential distribution of demographic groups and sex ratio (Garcia & Mantelatto, 2001; Chan & Williams, 2004; Andrade *et al.*, 2014, 2017; Silva *et al.*, 2018; Bernardes *et al.*, 2019; Sousa *et al.*, 2019).

Most decapod species in tropical regions present two types of reproduction: continuous, which occurs all year round (Costa & Negreiro-Fransozo, 1998; Reigada & Negreiros-Fransozo, 2000) and continuous with peaks in some periods (Bertini *et al.*, 2010*b*; Castilho *et al.*, 2015; Frameschi *et al.*, 2015). In temperate regions, reproductive cycles are frequently seasonal (Lancaster, 1990; Gherardi & Cassidy, 1995; Terossi *et al.*, 2010). However, Bauer (1992) stated that there is no general model to explain how long the reproductive periods of marine crustaceans last. Different species have distinct phylogenetic histories, peculiar reproductive capacities and restrictions imposed by body size. Moreover, at similar latitudes, there are variations in habitat characteristics and even other biotic and abiotic parameters that can influence reproductive patterns.

Temperature, salinity, sediment texture, occurrence of water masses, food availability and even the specific physiological needs of each life cycle phase can also modulate the ontogenetic distribution of brachyurans (Andrade *et al.*, 2015; Silva *et al.*, 2018; Theuerkauff *et al.*, 2018; Bernardo *et al.*, 2020). In this sense, we tested the hypothesis that there is differential occupation between the demographic groups of *L. ferreirae* in space and time.

Furthermore, given the importance of studies about population characteristics, especially those conducted before the MPA was established, we decided to investigate the population dynamics of *L. ferreirae* in the Ubatuba region, focusing on the frequency distribution of individuals in size classes, sex ratio and effect of environmental variables (temperature, salinity, texture and organic matter content in the sediment) on reproduction and recruitment.

Materials and methods

Sampling and study area

We captured crabs monthly from January 1998 to December 2000. A total of 480 trawl sets were performed in three bays at varying depths. Trawling was done on a fishing boat outfitted with double-rig nets, each area was trawled for 30 min and covered a total of $18,000 \, \text{m}^2$ per trawl. From 1998–1999, the Ubatumirim (UBM), Ubatuba (UBA) and Mar Virado (MV) Bays were sampled once a month. In each bay, six sampling stations were established: three in areas sheltered from the waves (5, 7.5 and 10 m deep), and three in exposed areas (10, 15 and 20 m deep) (Figure 1). The stations (except the 7.5 and 10 m depths) were positioned along transects that were parallel to the coastline. These stations were selected according to the following characteristics: their position relative to the bay's mouth, the presence of rocky shores or beaches along the bay's perimeter, freshwater inflow, proximity to offshore water, depth, and sediment texture. Similarly, the collections of 2000 were only carried out in Ubatuba Bay, at the 5, 10, 15 and 20 m sample stations.

At each station we collected bottom and surface water samples using a Nansen bottle, and measured salinity and temperature (°C) with an optical refractometer and a mercury thermometer, respectively. Sediment samples were collected with a Van Veen grab, from which we obtained sediment texture and organic matter content. Depth was measured with an echobathymeter connected to a Global Positioning System (GPS). Immediately after collection, we put the sediment samples into labelled plastic bags and froze them to minimize organic matter decomposition until further analyses.

In the laboratory, the sediment was dried at 70°C for 72 h in an oven. For the grain size composition analysis, two 50 g subsamples for each sampling station were separated, treated with 250 ml of NaOH solution $(0.2 \, \text{mol} \, l^{-1})$ and stirred for 5 min to release silt and clay particles. Afterwards, sub-samples were rinsed in a 0.063-mm sieve. The grain size was classified according to the Wentworth (1922) scale: >2 mm (gravel); 2.0–1.0 mm (very coarse sand); 1.0–0.5 mm (coarse sand); 0.5–0.25 mm (medium sand); 0.25–0.125 mm (fine sand); 0.125–0.063 mm (very fine sand), and smaller particles were classified as silt and clay.

Grain diameter was expressed in phi (φ) values (calculated from the formula $\text{phi} = -\log_2 d$, where d = grain diameter in mm), and the following classes were obtained: $-2 \leq \text{phi} < -1$ (gravel), $-1 \leq \text{phi} < 0$ (very coarse sand), $0 \leq \text{phi} < 1$ (coarse sand), $1 \leq \text{phi} < 2$ (medium sand), $2 \leq \text{phi} < 3$ (fine sand), $3 \leq \text{phi} < 4$ (very fine sand), and $\text{phi} \geq 4$ (silt and clay). From the cumulative distribution curves of these classes, the 16th, 50th and 84th percentiles were extracted and the mean diameter (md) was calculated using the formula: $\text{MD} = (\text{phi}_{16} + \text{phi}_{50} + \text{phi}_{84})/3$ (Suguio, 1973). The three most quantitatively important sediments were defined according

to Magliocca & Kutner (1965): Class A corresponds to sediments with medium sand, coarse sand, very coarse sand and gravel; class B is fine sand and very fine sand and class C is silt and clay.

The organic-matter content of the sediment at each sampling station was estimated as the difference between the initial and ash-free dry weights of three subsamples (10 g each) incinerated in porcelain crucibles at 500°C for 3 h (Hakanson & Jansson, 1983).

Biological data

The crabs were identified to species (Melo, 1996) and sex was determined by the shape of the abdomen (a thin shape for males and an oval shape for females) and the number of pleopods (two pairs for males and four pairs for females). The carapace width (CW) was measured with a 0.1 mm precision calliper.

Individuals were classified as juveniles or adults based on the examination of secondary sexual characters such as pleopod morphology, free abdomen (i.e. the abdomen does not adhere to the thoracic sternites), convex abdomen (forming an incubator chamber) in the females, and distinct cheliped development in adult males when compared with juvenile males. Such changes associated with sexual maturity are similar to those described for the epialtid *Epialtus brasiliensis* Dana, 1852 and *Acanthonyx scutiformis* (Dana, 1851) (Negreiros-Fransozo *et al.*, 1994; Teixeira *et al.*, 2009). The identification of juvenile specimens based on the abdominal condition (sealed or not) has been widely used for Portunoidea (e.g. Taissoun, 1969; Williams, 1974; Silva *et al.*, 2017; Sousa *et al.*, 2019) and is useful for the representatives of the superfamily Majoidea. Four demographic groups were used in the analyses: juvenile males and females (J), adult males (AM), non-ovigerous adult females (AF) and ovigerous females (OF).

All crabs were submitted to a macroscopic examination of gonads, and the stages of gonadal development were determined based on the shape, colour and size of the ovaries, testicles and vas deferens (Choy, 1988; Abelló, 1989). Four stages of gonadal development were established for males and females based on gonad size, shape and colour: (1) RU: rudimentary (males: uncoloured filamentous vas deferens; females: whitish, thin filamentous ovary); (3) ED: developing (males: small, white gonads, being smaller than the hepatopancreas; females: beginning of maturation, small yellow ovaries); (4) DE: developed (males: largest gonadal development size, white gonads; females: bright yellow ovaries filling almost the entire thoracic cavity) (Choy, 1988; Abelló, 1989). Females carrying embryos (fertilized eggs) adhered to the pleopods (ovigerous females – OF) were described in posterior analyses.

Data analyses

Bottom temperature and salinity (TS) diagrams were created to show the influence of the water masses in the study regions (Tomczak, 1999).

Tests for homoscedasticity (Levene tests) and normality (Shapiro–Wilk tests) were first performed as prerequisites for the statistical test ($P = 0.05$) (Zar, 1999). The variance analysis (ANOVA) and a posteriori Tukey test ($P < 0.05$) were used to compare surface and bottom temperature values (ST and BT, respectively), bottom salinity (BS), percentage of organic matter in sediment (OM) and phi among the sampling stations and seasons (summer from January to March; autumn from April to June; winter from July to September; and spring from October to December). All environmental factors were also compared between protected and exposed areas through Student's *t*-test ($P < 0.05$).

Modal values were determined for each CW frequency using the software PEAKFIT (Automatic Peak Fitting Detection and Fitting, Method I-Residual, no Data Smoothing).
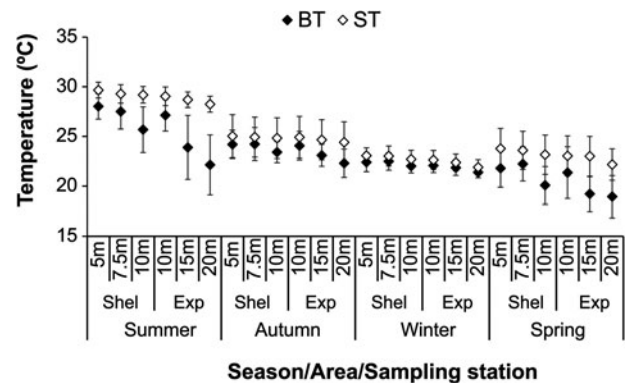

Fig. 2. Bottom and surface temperature, seasonal variation in each sampling stations and areas from 1998 to 2000 (BT, bottom temperature; Exp, exposed area; Shel, sheltered area; ST, surface temperature).

The CW of adult males and females was compared using the Student's *t*-test for two independent samples of parametric data. The Kolmogorov–Smirnov test was used to compare the size frequency distribution of males and females. Possible deviations from the expected 1:1 sex ratio in each size class were verified by the binomial test (Wilson & Hardy, 2002).

A contingency table with the abundance of demographic groups per season and bathymetric zone was created using a correspondence analysis (CA). To clearly visualize the correlation of abundance of each demographic group per season and bathymetric zone, each datapoint was plotted proportionally to the abundance in the contingency table.

The reproductive period was estimated based on the monthly frequency of DE females in relation to the total number of females. Similarly, recruitment was expressed by the monthly frequency of juveniles in relation to the total number of individuals.

Then, the collinearity between the environmental variables was verified, as recommended by Zuur *et al.* (2010). The relationship between the abundance of demographic groups and environmental parameters (BT, BS, OM and PHI) was evaluated with a Redundancy Analysis (RDA). The RDA is a multivariate statistical test that measures how strong the association between groups of variables is. The environmental parameters were included in the first group, and the abundance of juvenile males and females (J), adult males (AM), non-ovigerous adult females (AF) and ovigerous females (OF), were included in the second group. The RDA produces final coordination scores that summarize the linear relationship between the explanatory and response variables. Only environmental variables with coefficients greater than the module of ± 0.4 were considered biologically significant (Rakocinski *et al.*, 1996). The CA and RDA were performed using the 'ca' and 'vegan' packages (Nenadic & Greenacre, 2007; Oksanen *et al.*, 2013; R Development Core Team, 2020).

Results

The sampling areas exposed to wave action (10, 15 and 20 m) showed lower values of BT ($T = -5.254$; df = 430; $P < 0.001$; Figure 2). The mean BT in the exposed area was 22.2 ± 2.8°C. The highest variations among BT and ST values in the Ubatuba region occurred in summer and spring (Figure 2). During the autumn and winter there was no variation of BT and ST related to increased depth (Figure 2).

The area exposed to wave action presented the highest BS values ($T = 3.5456$; df = 430; $P < 0.001$; Figure 3). The BS mean in exposed areas was 34.6 ± 1.4‰. Seasonally, the highest values of BS occurred in the summer (34.9 ± 0.9‰) and autumn (35.4 ± 0.8‰) (ANOVA;
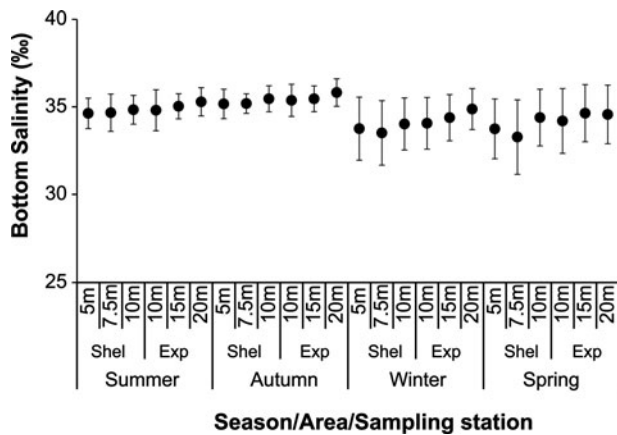
Fig. 3. Bottom salinity seasonal variation in each sampling stations and areas from 1998 to 2000 (Exp, exposed area; Shel, sheltered area).
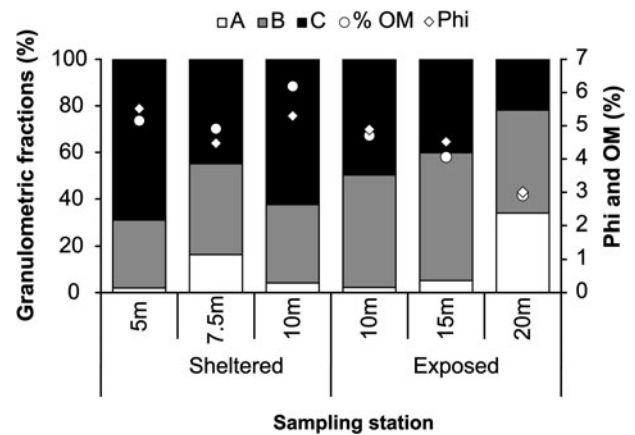

Fig. 5. Granulometric fractions, organic matter content and the mean of phi for each transect (grain-size classes (%): A, medium sand, coarse sand, very coarse sand and gravel; B, fine sand and very fine sand; C, silt + clay; %OM, percentage of organic matter content).
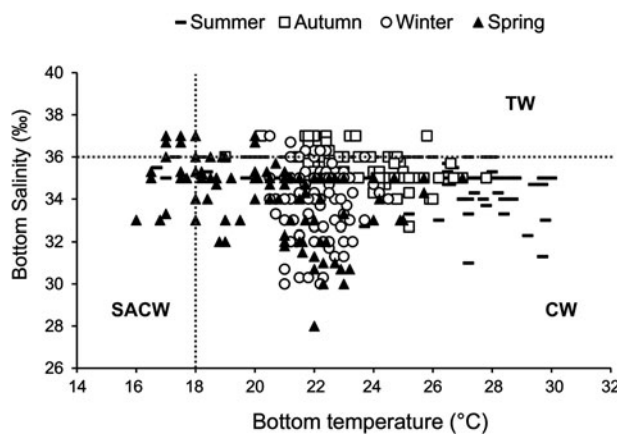

Fig. 4. Diagram showing the seasonal variation of water temperature and salinity from January 1998 to December 2000, in Ubatuba region, south-eastern coast of Brazil (CW, Coastal Water; TW, Tropical Water; SACW, South Atlantic Central Water).
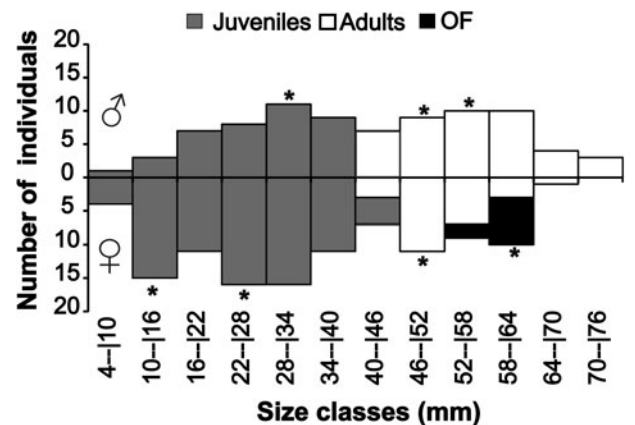

Fig. 6. *Libinia ferreirae* Brito Capello, 1871. Frequency distribution in size classes for males and females with indication of modal peaks in the Ubatuba region, São Paulo northern coast, Brazil (*, modal peaks).

Table 1. *Libinia ferreirae* Brito Capello, 1871

Demographic group	N	Min – Max (mm)	Mean ± SD (mm)
Juveniles	123	5.8–45.0	26.8 ± 10.2
Adult male	43	44.0–75.8	55.3 ± 8.6
Adult female	25	45.8–64.4	52.4 ± 5.2
Ovigerous female	31	45.7–63.2	54.1 ± 5.4

Number of individuals (N), size ranges, means and standard deviations of carapace width for each demographic group.
N, number; SD, standard deviations.

$F = 23.95$; df = 3; $P < 0.001$; Figure 3). Spatially comparing all sampling areas, the highest values of BS (ANOVA; $F = 4.553$; df = 5; $P < 0.001$), occurred at the 20 m deep site (35.1 ± 1.2‰; Figure 3).

In the study region, there were three water masses, which are typical in the region. The Coastal Water (CW) ($T \geq 20°C$; $S \leq 36$) predominated throughout the year; while South Atlantic Central Water (SACW) ($T \leq 18°C$; $S \leq 36$) and Tropical Water (TW) ($T \geq 20°C$; $S \geq 36$) presented high influence in the spring and autumn, respectively (Figure 4).

The features of the sediment (Phi and OM) differed among the sampled areas (Phi – $F = 90.64$; df = 5; $P < 0.001$; OM – $F = 13.35$; df = 5; $P < 0.001$). In all study periods, the lowest mean OM (3.3%) ($P < 0.001$) was at 20 m depth, with a mean Phi value equal to 3.0 (Figure 5).

A total of 222 individuals of *Libinia ferreirae* were captured, comprising 123 J (males and females), 43 AM, 25 AF and 31 OF. The CW of adult males and adult females (AF and OF) was not significantly different ($T = -0.8561$; df = 153; $P = 0.393$).

The mean CW of each demographic group, along with standard deviation and range, are shown in Table 1. The size-class frequency distribution was polymodal for both sexes (Figure 6). The highest abundance of J occurred in the fourth (22–|28 mm CW) and fifth size class (28–|34 mm CW). Adult males and females were more abundant in the eighth size class (46–|52 mm CW).

In the total population, the sex ratio (M: F) was 1:1.6 ($P < 0.05$); among size classes, a female-biased sex ratio was only seen in the 10–|16 mm CW (Table 2). The frequency per

size class was not significantly different between males and females (dmax = 0.122; df = 2; $P = 0.08$).

Most of the sampled population was composed of J, concentrated in the shallower sample areas, such as 5 and 7.5 m of depth. The adults (males and females, mainly ovigerous) had a high association with deeper areas, especially at 15 m (Figure 7).

Both the reproductive and recruitment periods were continuous with peaks (Figure 8). Reproductive males and females were found in all seasons. Even though all demographic groups were found during the entire survey, except J, the temporal distribution based on the CA analysis (Figure 9), indicated a relationship

Table 2. *Libinia ferreirae* Brito Capello, 1871

Size class (mm)	Juveniles			Adults			Total of crabs		
	♀	♂	P	♀	♂	P	♀	♂	P
4 —| 10	4	1	0.37	0	0	–	4	1	0.37
10 —| 16	15	3	0.01*	0	0	–	15	3	0.01*
16 —| 22	11	7	0.45	0	0	–	11	7	0.45
22 —| 28	16	8	0.15	0	0	–	16	8	0.15
28 —| 34	16	10	0.55	0	0	–	16	10	0.55
34 —| 40	11	9	0.82	0	0	–	11	9	0.82
40 —| 46	7	5	0.17	4	7	0.17	11	12	1.00
46 —| 52	0	0	–	22	9	0.06	22	9	0.06
52 —| 58	0	0	–	16	10	0.32	16	10	0.32
58 —| 64	0	0	–	13	10	0.67	13	10	0.67
64 —| 70	0	0	–	1	4	0.37	1	4	0.37
70 —| 76	0	0	–	0	3	0.25	0	3	0.25
Total	80	43	<0.01*	56	43	0.15	136	86	<0.01*

Distribution of individuals in size classes and demographic group.
*, statistical difference ($P < 0.05$).
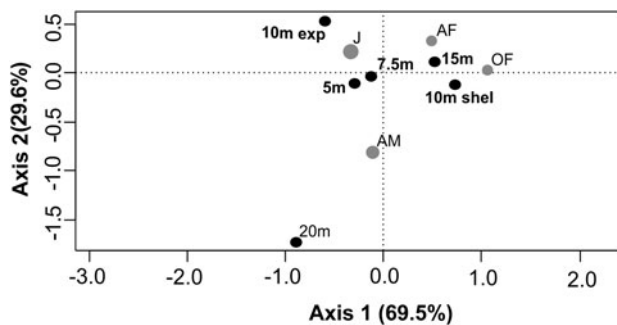
Fig. 7. *Libinia ferreirae* Brito Capello, 1871. Correspondence analysis (CA) of the abundance of demographic groups in the sampling stations sampled in the Ubatuba region. At the bottom the statistical summary of Pearson's χ^2 test for randomness of the observed association (AF, adult females; AM, adult males; Exp, exposed; J, juveniles; OF, ovigerous females; Shel, sheltered).

between J and spring, and between female adults (AF and OF) and summer and autumn.

According to the RDA axis 1, which explained 94% of the variance, the abundance of J, AM and AF was inversely proportional with BT and BS, while OF had a proportional relationship with BT and BS (Figure 10).

Discussion

The results of this study revealed the absence of size sexual dimorphism among adults of *Libinia ferreirae* and a sex ratio favouring females, even though most brachyuran crab species have sex ratios close to 1:1 (Hartnoll, 1978).

Sexual dimorphism with larger males than females seems to be a common pattern for crustaceans, including brachyurans and crayfishes (Miazaki *et al.*, 2019; Sousa *et al.*, 2019; Bernardo *et al.*, 2020; Hamasaki *et al.*, 2020). According to Hartnoll (1969), males are larger because they tend to protect pre- and post-moulting females with the copulatory embrace, representing an adaptation to ensure reproductive success. However, the average size of *L. ferreirae* males and females did not differ significantly herein.
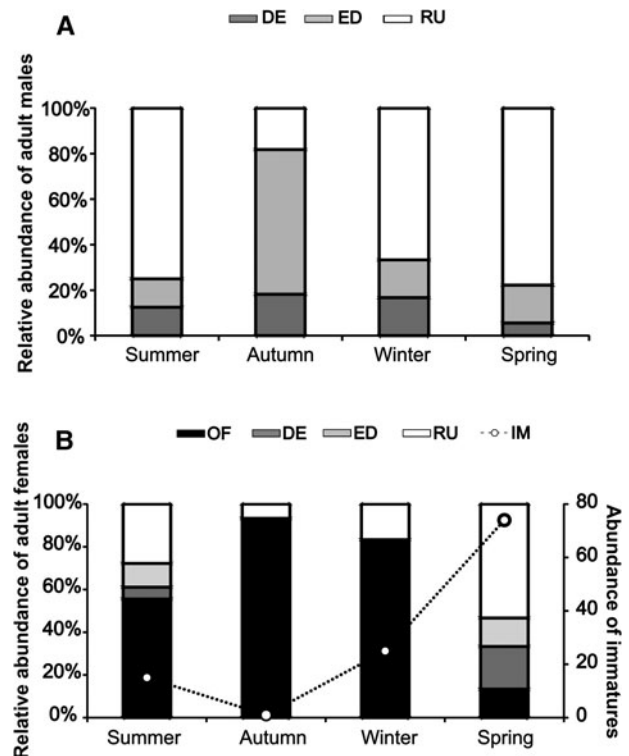
Fig. 8. *Libinia ferreirae* Brito Capello, 1871. Seasonal variation in the proportion of individuals in different gonadal stages in the Ubatuba region: (A) males; (B) females (DE, developed gonads; ED, developing gonads; IM, immatures; OF, ovigerous females; RU, rudimentary gonads).

Sexual dimorphism seems to be a variable characteristic within *Libinia*. Studies about the population characteristics of *Libinia dubia* H. Milne Edwards, 1834 (Able *et al.*, 1999) and *L. ferreirae* (Gonçalves *et al.*, 2016a) showed that there was no difference in size between the sexes for the former species (Able *et al.*, 1999), while females were larger than males in the latter (Gonçalves *et al.*, 2016a). On the other hand, males of *L. emarginata* Leach, 1815 and *L. spinosa* were significantly larger than females
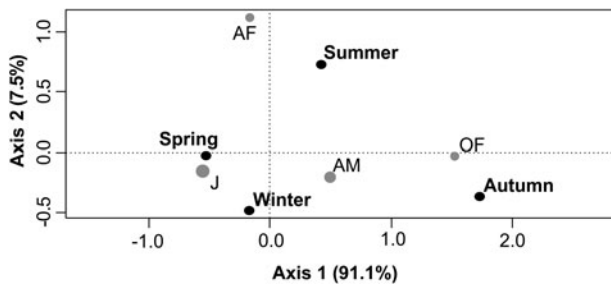
Fig. 9. *Libinia ferreirae* Brito Capello, 1871. Correspondence analysis (CA) of the abundance of demographic groups in the seasons in 1998 and 2000 sampled in the Ubatuba region (AF – adult females; AM, adult males; J, juveniles; OF, ovigerous females).
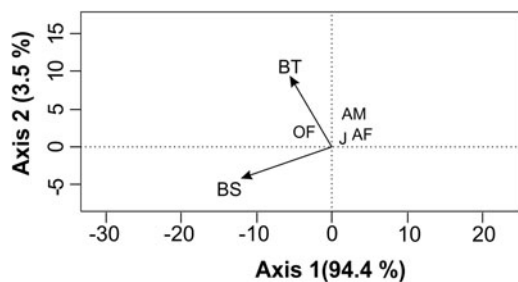
Fig. 10. *Libinia ferreirae* Brito Capello, 1871. Results from the redundancy analysis (RDA): ordination of the first two canonical axes, with environmental variable data and demographic categories abundance in the Ubatuba region. Coefficients greater than the module of ± 0.4 were considered ecologically relevant (Rakocinski *et al.*, 1996) and are shown in the plot (BT, bottom temperature; BS, bottom salinity; AF, adult females; AM, adult males; J, juveniles; OF, ovigerous females).

(Able *et al.*, 1999; Sal Moyano *et al.*, 2011). The sex ratio for *Libinia* also seems to be variable, e.g. adults in the present study had a proportion of 0.8♂:1♀ (Table 2); *L. dubia* 1.3♂:1♀ (Able *et al.*, 1999); *L. ferreirae* from Cananéia 0.5♂:1♀ (Gonçalves *et al.*, 2016a); *L. emarginata* 2.5♂:1♀ (Able *et al.*, 1999) and *L. spinosa* 1.5♂:1♀ (Sal Moyano *et al.*, 2011). These results suggest that dimorphism related to size and sex ratio may be closely related, with males tending to be larger than females in populations where they are more abundant.

Similarly, there was no sexual dimorphism found for *Achelous spinimanus* (Latreille, 1819) in Macaé, on the coast of Rio de Janeiro (Andrade *et al.*, 2017) and *A. spinicarpus* (Stimpson, 1871) in the region of Ubatuba and Caraguatatuba (Silva *et al.*, 2017), with all these studies showing female-biased sex ratios. In addition, some authors have pointed out that trawling (as used in the present study) is the most reliable collection method for characterizing population aspects (Able *et al.*, 1999).

The frequency distribution by size revealed that both sexes in the population of *L. ferreirae* from the Ubatuba region have polymodal distributions. This type of classification indicates the presence of two or more age groups, or that these differences in frequency are related to differential migration, mortality and/or birth rates (Diaz & Conde, 1989). In the sampled population, most peaks could be associated with the differential displacement of the demographic groups, since juveniles of *L. ferreirae* can live in association with jellyfish *L. lucerna* (Gonçalves *et al.*, 2017), while brachyuran OFs migrate to deeper areas to optimize larval dispersion and survival (Abelló, 1989; Andrade *et al.*, 2014; Bernardes *et al.*, 2019).

This symbiotic relationship between *L. ferreirae* and jellyfish may also explain the lower CW values of juveniles from Cananéia (Gonçalves *et al.*, 2017), compared with the same group in the present study. During trawls in Cananéia, jellyfish

were examined for the presence of crabs (Gonçalves *et al.*, 2017), consequently there were a lot of small individuals. Due to the low number of jellyfishes in the Ubatuba region (Gonçalves *et al.*, 2016b), they were not sampled. However, despite the absence of *L. lucerna*, the studied area also seems to favour species recruitment, since juveniles corresponded to around 60% of the crabs sampled.

In Cananéia, from February 2013 to January 2014, the average size of adults was also lower (AM = 37.8 mm; AF = 42.1) (Gonçalves *et al.*, 2016a) when compared with adults in the Ubatuba region (AM – 55.3 ± 8.6 44.0; AF – 53.6 ± 5.4). The larger size of the individuals could be associated with the fact that the sampling was performed at a time when there was less intense fishing activity (1998–2000). The number of productive units (fishermen and vessels) in São Paulo State in 2013 was double that of 1998 (Instituto de Pesca, São Paulo), consequently, the populations of species associated with by-catch, such as *L. ferreirae*, are impacted by this activity as mortality rates tend to be higher in adults and the sooner individuals reach maturity, the greater their reproductive gain. Therefore, fishing pressure can cause individuals to reach maturity at smaller sizes, which can reduce fecundity and reproduction rates (Keunecke *et al.*, 2012).

In addition to fishing activity, there are other factors that can change the size of individuals, e.g. temperature. Several rules have been proposed from numerous observations and comparisons of specimens from different latitudes (Vernberg, 1962; Blackburn *et al.*, 1999). One such rule is that of Jame, which suggests that the smallest individuals of a species are generally found in geographic areas with higher temperatures, i.e. in regions with lower latitudes. Conversely, larger specimens will be collected in colder regions, at higher latitudes (Blackburn *et al.*, 1999). This probably occurs because lower temperatures require lower metabolic rates, which leads to lower energy expenditure, thus facilitating the accumulation of reserves and the acquisition of larger body sizes. In addition, colder waters tend to have higher productivity, which would also support larger body sizes.

When comparing the size variation of *Libinia* OFs from Argentina with that of the present study (45.7–63.2 mm CW), we note that Jame's rule did not apply. In Mar del Plata, Argentina (38°S 57°33′W), OF size ranged from 40.0–56.0 mm CW (Sal Moyano *et al.*, 2011) and in Cracker Bay, Patagonia-Argentina (42°56′S 64°21′W) this variation was 41.9–62.7 mm CW (González-Pisani & López Greco, 2014). These results could be consequences of countergradient variation, which is based on the fact that individuals of a given species can reproduce and grow at the same temperatures, regardless of latitude, simply by restricting these physiological activities to the appropriate portion of the temperature cycle. In this case, the duration of the growing season (instead of the temperatures at which growth occurs) would decrease with increasing latitude (Conover & Present, 1990). The authors also propose that if the growth rates of organisms in environments with short growing periods exceed those of environments with long growing periods, the duration of the growth phase will be compensated at all temperatures that allow development. This has been evidenced by several marine invertebrates (Levinton, 1983; Lonsdale & Levinton, 1985), including another Majoidea: *Chionoecetes opilio* (O. Fabricius, 1788) (Burmeister & Sainte-Marie, 2010).

Countergradient variation was also observed for jellyfish that have a symbiotic relationship with *Libinia* spp. When comparing the diameter of jellyfish at different latitudes, such as Mar Chiquita, Argentina (37°45′S 57°26′W) (Zamponi, 2002); Rio de La Plata, Argentina/Uruguay (35°S 57°W) (Sal Moyano *et al.*, 2012); Punta del Este, Uruguay (34°58′S 54°57′W) (Vaz Ferreira, 1972); Paraná, Brasil (25°55′S 48°35′W) (Nogueira Jr & Haddad, 2005); Cananéia (25°04′S 47°50′W) (Gonçalves *et al.*,

2016*b*); Macaé (22°22′S 41°46′W) (Gonçalves *et al.*, 2016*b*) and in Paraíba (06°58′S 34°51′W) (Baeza *et al.*, 2017), we noticed that the average diameter of jellyfish was similar at all localities.

The sex ratio favouring females in the present study could be associated with the fact that Majoidea females do not require periodic copulations, since they can store sperm and spawn several times with just one sperm mass from a single copulation (González-Gurriarán *et al.*, 1998). Cananéia also presented the highest amount of *L. ferreirae* females in the population (Gonçalves *et al.*, 2017), with these authors highlighting differential occupation of habitats between the sexes as a justification for such a result.

In the Ubatuba region, there was differential occupation between juveniles and adults of *L. ferreirae* throughout the study period. The grouping of immatures in the shallowest sites, especially at 5 and 7.5 m depth, could be associated with the fact that these sites have greater availability of calcium-rich food, such as shell fragments (Almeida *et al.*, 2012). Moulted crabs are often found on hard substratum in shallow waters where they feed on calcium-rich organisms such as mussels and barnacles (Karlsson & Christiansen, 1996). In addition, the 7.5 m deep sampling area is naturally excluded from fishing, likely contributing to the abundance of individuals. The habitat complexity in areas less impacted by fishing is typically preserved, which favours the establishment of new individuals (Kaiser *et al.*, 2002).

The inversely proportional abundance of juveniles with BT and SF values may be related to peak recruitment during SACW entrance ($T \leq 18°C$; $S \leq 36$) in the spring. This water mass is characterized by low values of salinity and temperature, besides being responsible for the enrichment of water in coastal regions, and increasing primary productivity (Castro-Filho *et al.*, 1987). Subsequently, the high phytoplankton density sustains a large abundance of Salpas (Tunicata, Salpidae) and other invertebrate groups, whose carcasses and fecal pellets transfer organic matter to the sediment, benefiting benthic organisms (Pires-Vanin *et al.*, 1993). In this sense, the physicochemical characteristics of SACW are probably the real modulators of *L. ferreirae* recruitment in our study region. Other studies have also pointed to the higher supply of food as a modulating factor for the abundance of *L. ferreirae* (Gonçalves *et al.*, 2017) and other brachyurans, such as *L. spinosa* (Braga *et al.*, 2007), *H. pudibundus* (Bernardes *et al.*, 2019) and *A. spinimanus* (Sousa *et al.*, 2020).

The higher abundance of adults, mainly AF and OF, at greater depths may have occurred because of the behavioural pattern of crustaceans with planktotrophic larval stages. In places far from the coast, larval dispersion and survival are optimized since larval dispersion is facilitated by ocean currents in deeper regions (Andrade *et al.*, 2014) and because environmental conditions are stable, physiological stress in larvae is reduced (Abelló, 1989). Bernardes *et al.* (2019) suggested that the OFs of *H. pudibundus* are generally found in deeper areas due to the fact that salinity is higher, which favours embryonic development during incubation. Additionally, these authors suggested that this group moves away from the coast because their larvae float more easily in higher salinities.

Herein, a continuous reproductive period was found for *L. ferreirae*. Extensive reproductive periods are characterized by various spawning events throughout the year (Giese, 1959). When analysing *L. emarginata* and other Majoidea as *Chionoecetes opilio* and *Maja squinado* (Herbst, 1788), it has been found that OFs can also copulate, since their gonads are already developed and they can store new sperm masses, with females being able to spawn up to four times in a row (Hinsch, 1968; Elner & Beninger, 1995; González-Gurriarán *et al.*, 1998). The same pattern was found in Cananéia for this species (Gonçalves *et al.*, 2017), with

continuous reproduction being a common feature of tropical and subtropical marine brachyurans such as: *L. spinosa* (Braga *et al.*, 2007), *Persephona mediterranea* (Herbst, 1794) (Bertini *et al.*, 2010*b*), *C. ornatus* (Andrade *et al.*, 2014), *Arenaeus cribarius* (Lamarck, 1818) (Silva *et al.*, 2018) and *H. pudibundus* (Miazaki *et al.*, 2019).

However, in Cracker Bay, Patagonia-Argentina (42°56′S 64° 21′W), individuals from the same genus reproduce seasonally, mainly in periods with higher temperatures and food availability (González-Pisani, 2011). These results corroborate the latitudinal effect paradigm, which states that reproduction can be continuous in tropical regions (lower latitudes) due to constant environmental conditions that favour gonadal development, feeding and spawning, while in temperate regions at higher latitudes, reproduction is generally restricted to a few months due to resource limitation and temperature variation (Bauer, 1992). Thus, we can infer that the reproductive pattern of *Libinia* is related to latitude, i.e. its metabolism could depend on the region where it is, affecting its reproductive characteristics.

We believe that the OFs of *L. ferreirae* peaked in the autumn in order to maximize their reproductive success, as there is higher food availability during this season. During this time of the year, the SACW usually recedes and there is intense suspension of sediments, causing a carriage with particulate organic matter generated in the previous period and, although crabs feed on bivalves and gastropods, they also consume the organic matter in the sediment (Gonçalves *et al.*, 2020). The mechanisms used by *L. ferreirae* to expand reproductive success in the present study were probably successful since there was 'effective spawning' in the region. This term refers to situations in which there is a peak in the number of juveniles soon after a peak in the abundance of reproductive individuals, making it possible to prove that reproductive individuals in a given period generated offspring in the following months (Crocos & Van der Velde, 1995).

Some of the characteristics of the population observed herein indicate that *L. ferreirae* uses the Ubatuba region throughout its entire life cycle. These features include continuous reproduction, high abundance of immature individuals and the presence of individuals at all stages of gonadal development. Therefore, direct and indirect changes in the region should be monitored to prevent damaging stocks of this species and others that are caught as by-catch. Furthermore, this study provides a basis in which to compare current data and also attests to the effectiveness of conservation strategies implemented in 2008–2009 for this species.

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